

Newts (*Triturus*, Salamandridae, Urodela) of the Bukovica and Ravni Kotari regions

(Yugoslavia)

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We studied highly allotopic distribution pattern of the smooth newt (*Triturus vulgaris*) and the alpine newt (*Triturus alpestris*) in Ravni Kotari and Bukovica regions (North Dalmatia). The zoogeographical impication(s) of such distribution patterns was analysed also. Facultative paedomorphosis was found in four alpine newt populations from Bukovica region, while in Ravni Kotari-paedomorphosis was recorded in one population of the smooth newt. Variability of eight morphometric characters (expressing overall size relations, locomotion abilities, and feeding abilities), as well as, sex ratio were studied separately for paedomorphic and metamorphic newts of three population samples of the alpine newt and one population sample of the smooth newt.

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Introduction

Studying newt (genus *Triturus*) populations and taxa inhabiting Mediterranean areas of Yugoslavia offers many opportunities such as pronounced morphological and genetical differentiation, unusual habitat sites, and frequent occurrence of paedomorphosis.

All three newt species that live in Yugoslavia can be found in Mediterranean areas. The smooth newt (*Triturus vulgaris*) is the most widespread; it inhabits some of the large islands (e. g. Cres, Krk) also. A pronounced morphological (Schmidtler and Schmidtler 1983) and genetical differentiation (Kalezić 1984) of the smooth newt taxa were observed in these areas which appeared to be linked with dynamic changes of physical and biotic conditions during Pleistocene times. The alpine newt (*Triturus alpestris*) was known only from mountains laying along the coast (Kolombatović 1902, 1907, 1908; Schmidtler 1988; authors' data, unpubl.). That the crested newt (*Triturus cristatus*) can be found in the most north-western part of the area in question is well known. Additionally, this species has been recorded recently in the most southeastern part (around Cetinje and Ulcinj, Montenegro; Džukić and Jovanović, unpubl.; Džukić and Kalezić, in press).

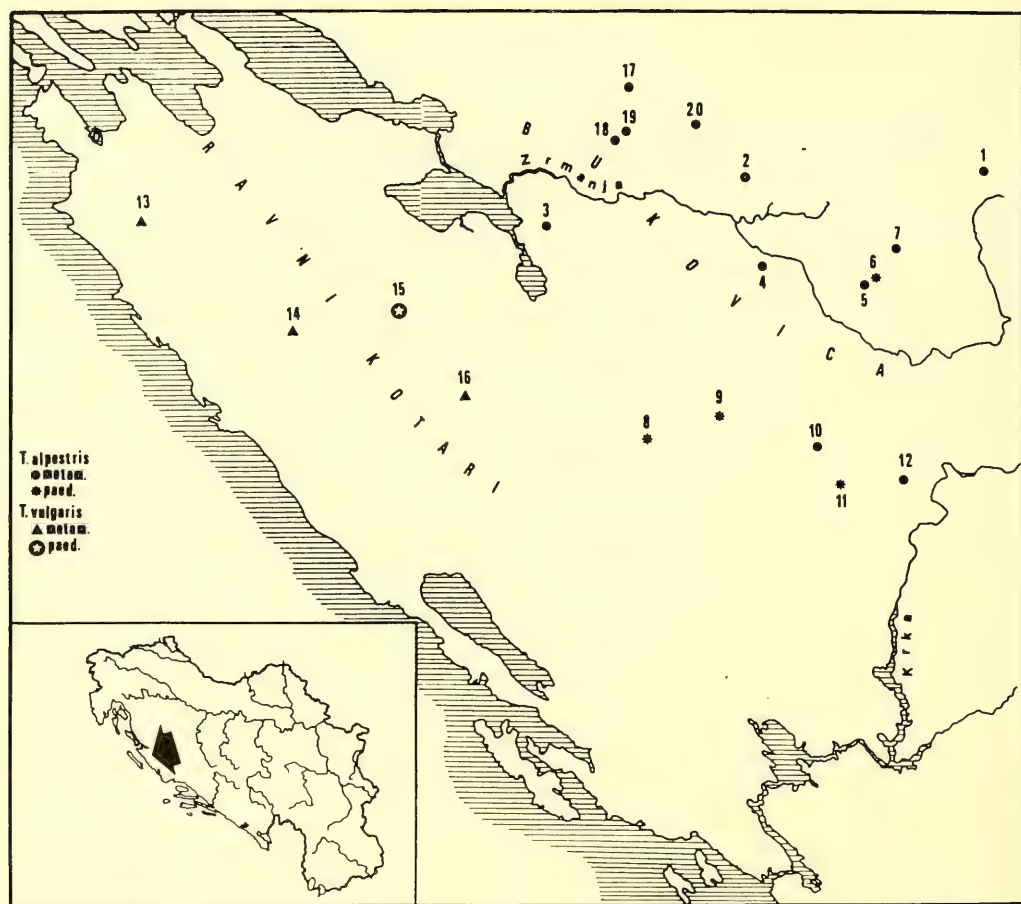


Figure 1. Survey of the localities (with altitudes) from which the material analysed originated. 1. Mala Popina, 603 m; 2. Veselinovići, 480 m; 3. Kruševo, 150 m; 4. Žegar, 80 m; 5. Urukolovac, 265 m; 6. Pajića Lokva, 275 m; 7. Čengići-Jurišići, 260 m; 8. Brgud, 260 m; 9. Kalanji, 320 m; 10. Matijevići, 260 m; 11. Grulovići, 245 m; 12. Rudelji, 240 m; 13. Bokanjačko blato, 20 m (Kolombatović 1908; Scherer 1902; Wolterstorff 1914; author's data); 14. Donji Zemunik, 80 m (Schmidtler and Schmidtler 1983); 15. Smilčić, 190 m; 16. Benkovac (8 km NW), 150 m (Schmidtler and Schmidtler 1983); 17. Mila voda, 810 m; 18. Čaber, 740 m; 19. Križ, 690 m; 20. Obli kuk, 850 m.

We are concentrated here on Bukovica and Ravni Kotari regions situated between mountain Velebit, the river Krka, and the Adriatic Sea. Two newt species live in these areas; the alpine newt occupies Bukovica, while the smooth newt can be found in Ravni Kotari. (The scoring of the crested newt from Bokanjačko blato of Scherer (1902) is still under the question). To the smooth newt populations from Ravni Kotari a subspecific status was attached, *T. v. schreiberi* (Wolterstorff 1914; see also Bischoff 1977). However, most recent studies on morphological (Schmidtler and Schmidtler 1983) and genetical differentiation (Kalezić et al. 1987) proved that, in spite of isolation from the main body of nominotypical subspecies range, populations from Ravni Kotari belong to *T. v. vulgaris*. In Bukovica and Ravni Kotari a number of the newt's populations appeared to be paedomorphic which proved again that the Mediterranean area is an important centre of the newt paedomorphosis (Kalezić and Džukić 1985, 1986).

The goal of this paper is two-fold: (1) to present and discuss highly allotopic distributions of the smooth and alpine newts in these regions, including the zoogeographic implication(s) of such distribution pattern, and (2) to give additional data on morphometric variability and sex ratio of the paedomorphic populations found in Bukovica and Ravni Kotari.

Study Areas and Methods

Bukovica region covers about 820 km² of North Dalmatia. It is situated between Velebit mountain and the river Krka (western and eastern boundaries) and Ravni Kotari (Figure 1). Bukovica is mainly karst plateau with 250 to 300 m of altitude (highest point 674 m). The landscape is typical holokarst with rare surface water bodies which usually appear at the sites of sinkholes and potholes with impermeable bottoms. The climate of Bukovica is a mixture of moderate continental and adriatic mediterranean climatic types; annual average precipitation ranges from 1000 to 1250 mm (Bertović 1975). Vegetation is mainly *Quercus-Caprinetum orientalis* association. Association *Ostrya-Quercetum pubescentis* is restricted to the narrow topogeographically higher belt of mountain Velebit (Trinajstić 1977, 1978).

Ravni Kotari is larger region (1180 km²) and quite different in respect to many landscape elements, such as nature of soil, altitude, water economy, etc. than Bukovica. It is mainly flysh plateau (highest point 413 m) which decline gradually to Nin and Ljubač Bays. Vransko Jezero is the largest open water body in Ravni Kotari and is situated just near to the Sea (Figure 1). Initially, Bokanjačko Blato and Nadinsko Blato were depressions where atmospheric water drained making large marshlands quite suitable as amphibian spawning sites. Unfortunately, Ravni Kotari has been changed drastically in last thirty years becoming mostly cultivated area. Bokanjačko Blato and Nadinsko Blato were drained and now used intensively for agriculture. The same happened with other swamped areas and watering-places, so many amphibian natural habitats were devastated. Many dug holes, used as water supply sites for agricultural purposes, replaced to some extent old amphibian breeding ponds, but undoubtedly changes in landscape elements of Ravni Kotari reduced drastically amphibian populations. Ravni Kotari has a variant of Adriatic mediterranean climate type; there is a secondary maximum of precipitation falling in early spring or early summer. The average annual precipitation ranges from 900 to 1000 mm (Bertović 1975). A narrow coastal zone has Eumediterranean's *Orno-Quercetum ilicis* belt, while the rest of Ravni Kotari is covered with *Quercus-Caprinetum orientalis* association (Trinajstić 1977, 1978).

Occurrence of newts and other amphibian species were investigated by looking for spawning sites during spring periods of the years 1985, 1986, 1987 and 1989. (Newts were caught with a fisherman net by more or less random sweeps or when newts surfaced.) We sampled three alpine newt populations (Žegar, Pajića Lokva and Grulovići) and a smooth newt population (Smilčić) much more intensively than other populations because they were more densely populated and more accessible for collecting. The sinkhole near Žegar village, at the altitude of 80 m above sea level, is a pond 25 m wide and about 30 m long. The pond bottom is heavily covered with deep mud. Only metamorphosed alpine newt individuals were found in this pond. Pajića Lokva, near Macure village, and the pond in Grulovići village are transformed elliptic sinkholes (Pajića Lokva is 14 m wide and 22 m long, while pond Grulovići is 30 m wide and 35 m long). In both ponds here was a great deal of submerged vegetation, mainly buttercup and green algae. The altitude of Pajića Lokva is 275 m above sea level, and in this pond, during sampling in 1985 year, only paedomorphic newts were found. Local people took advantage of severe droughts during summer months of that year and cleaned the pond of the mud. Next year (1986) only a few metamorphosed alpine newts were observed in this water body. Same happened with Grulovići locality; the pond was completely rid of the mud five years ago. (The altitude of the pond in Grulovići is 245 m above sea level). The smooth newts from Smilčić were collected from a few holes dug nearby. The bottom of the holes were mainly overgrown with *Chara* spp. The altitude of Smilčić is 190 m above sea level. A fore years inspection of these holes revealed that they were differently populated with newts and that the number of newts differed annually.

Adult newts were recognised by size and, in the case of suspected individuals, by gonadal inspection. Specimens from Žegar, Pajića Lokva, Grulovići and Smilčić localities were conserved in 70 % ethanol and measured for the following morphometric characters: L—total length, L_{sv}—snouth-vent length (measured from the snouth to the posterior edge of cloaca basis), L_{cd}—tail length (measured from the anterior edge of the cloaca basis to the tip of the tail), L_{tc}—head width, L_c—head length (measured from the snout to the corner of the mouth), P_a—forelimb length, P_p—hindlimb length, D—distance between fore and hind limbs. When a number of newt were collected no more than fifty randomly chosed specimens of each sex were measured. Different statistical analyses were performed according to procedures suggested by Sokal and Rohlf (1981).

Results

Inventory of 40 possible amphibian spawning sites in Bukovica region yielded 16 sites with the alpine newts and none with the smooth newts (Figure 1). Paedomorphic individuals of the alpine newt were found in 4 populations (Pajića Lokva, Grulovići, Brgud and Kalanji). Other amphibian species found here were as follows: *Bufo bufo*, *Bufo viridis*, *Rana ridibunda*, *Rana dalmatina*, *Hyla arborea*, *Salamandra salamandra* and *Proteus anguinus*. In Ravni Kotari region of 9 possible amphibian spawning sites, the smooth newt was found in 2 sites and none of the alpine newt was observed (Figure 1). Paedomorphic smooth newts were found only in Smilčić population sample. Other amphibian species in Ravni Kotari were: *Bufo bufo*, *Bufo viridis*, *Rana ridibunda*, *Rana dalmatina* and *Hyla arborea*.

The incidence of paedomorphic individuals in some alpine newt populations is very high. In Pajića Lokva of 112 captured newts all were paedomorphic (Table 1). The percentage of paedomorphic individuals in Grulovići sample is also very high (92 %), much higher than in some well known paedomorphic alpine newt populations (Bukumirsko Jezero, for example; Kalezić et al. 1989). Out of 83 smooth newt adults from Smilčić, 50 individuals were paedomorphic (60 %). Among paedomorphic newts females outnumber males considerably in all three population sample (Table 1). The same trend was observed for some other alpine newt paedomorphic populations (Kalezić et al. 1989), and smooth newt paedomorphic populations (Kalezić and Džukić 1986). Among metamorphic newts such sex ratio imbalance was not found (Table 1).

Table 1. Numbers of paedomorphic and metamorphic newts from one *T. vulgaris* population sample, and from three *T. alpestris* population samples. F-females, M-males.

| | Paedomorphic | | Metamorphic | |
|---------------------|--------------|----|-------------|----|
| | F | M | F | M |
| <i>T. vulgaris</i> | | | | |
| Smilčić | 42 | 8 | 19 | 14 |
| <i>T. alpestris</i> | | | | |
| Pajića lokva | 86 | 26 | 0 | 0 |
| Grulovići | 43 | 1 | 2 | 2 |
| Žegar | 0 | 0 | 37 | 29 |

Tables 2, 3 and 4 include the mean values of eight morphometric characters and their coefficients of variation for females and males of paedomorphic and metamorphic newts separately. (Morphometric characters were ordered in Tables in the manner that characters expressing overall-size relations (L , L_{sv} , D) were put the first following by characters connected with locomotion abilities (P_a , P_p , L_{cd}), and characters connected with feeding abilities (L_{ic} , L_c .) The result of univariate analysis of variance, which was performed to test differences between paedomorphic and metamorphic individuals with respect to character means, are also shown in Tables 2 and 5. Intrapopulation comparison between paedomorphic and metamorphic individuals (Smilčić sample, Table 2) showed for most characters paedomorphic females appeared to be somewhat bigger in size than metamorphic individuals of the same sex. Highly statistically different were characters connected with feeding abilities – paedomorphic females had much more wider and shorter head than metamorphic females. Paedomorphic-metamorphic comparison between males of the same population showed less pronounced differences in size components (Table 2). The exception was head length where paedomorphic males had significantly shorter head than metamorphic individuals. For most characters, females showed the greatest paedo-

Table 2. Means (\bar{X}), standard errors (\pm SE), CV-coefficient of variation (%), and ANOVA F-ratios between paedomorphic and metamorphic newts from Smilčić locality. N-sample size. ^{*}P<0.05, ^{**}P<0.01, ^{***}P<0.001.

| | | | L | L _{sv} | D | P _a | P _p | L _{cd} | L _{tc} | L _c |
|-----------------------|-----------------|-----------------|-------|-----------------|-------|----------------|----------------|-----------------|-----------------|----------------|
| Paedomorphic newts | ♀♀ (N = 42) | \bar{X} | 65.48 | 35.51 | 19.16 | 11.22 | 11.31 | 34.15 | 6.81 | 4.15 |
| | | \pm SE | 1.54 | 0.62 | 0.42 | 0.20 | 0.26 | 0.43 | 0.13 | 0.06 |
| | | CV | 12.91 | 11.31 | 14.18 | 11.72 | 14.73 | 6.85 | 12.41 | 9.56 |
| | ♂♂ (N = 8) | \bar{X} | 67.24 | 34.28 | 17.80 | 12.85 | 13.49 | 36.59 | 6.17 | 4.26 |
| | | \pm SE | 1.88 | 0.50 | 0.51 | 0.39 | 0.55 | 1.35 | 0.13 | 0.18 |
| | | CV | 7.42 | 4.10 | 8.15 | 8.54 | 11.50 | 9.77 | 5.95 | 12.16 |
| Metamorphic newts | ♀♀ (N = 19) | \bar{X} | 61.49 | 32.43 | 17.63 | 10.65 | 10.52 | 31.54 | 6.09 | 4.61 |
| | | \pm SE | 1.61 | 0.97 | 0.36 | 0.26 | 0.25 | 1.10 | 0.10 | 0.08 |
| | | CV | 10.11 | 13.08 | 8.81 | 10.81 | 10.25 | 13.51 | 7.27 | 5.91 |
| | ♂♂ (N = 14) | \bar{X} | 68.12 | 34.65 | 16.93 | 12.76 | 12.84 | 37.63 | 5.87 | 4.77 |
| | | \pm SE | 1.31 | 0.45 | 0.49 | 0.46 | 0.47 | 1.17 | 0.09 | 0.07 |
| | | CV | 6.08 | 4.88 | 10.87 | 13.64 | 13.83 | 9.87 | 5.88 | 5.84 |
| | (df = 60) | F _{♀♀} | 2.85 | 2.90 | 4.91 | 2.50 | 3.53 | 2.79 | 11.37 | 18.82 |
| (df = 21) | F _{♂♂} | 0.18 | 3.54 | 3.79 | 0.02 | 0.73 | 2.98 | 3.61 | 9.14 | |

morphic-metamorphic differences (Table 2) which did not happen in the smooth newt population sample from Velika Osječenica (Crna Gora) where F-ratio values appeared to be higher in males than in females (Tucić et al. 1985). Also, in this population for all analysed characters and for both sexes metamorphic individuals were considerably larger in size than paedomorphic ones.

The variability level of characters (CV values) studied in Smilčić population sample differed substantially, from 14.7 % for the forelimb length to 4.1 % for the snouth-vent length (Table 2). With respect to sex differences, females appeared to be more variable than the males in both paedomorphic and metamorphic group of individuals. This difference was statistically significant in paedomorphic group ($t = 2.48$, $df = 14$, $P < 0.05$), but not in metamorphic group ($t = 0.69$, $df = 14$). (Unweightes

Table 3. Collection localities, means (\bar{X}), standard errors (\pm SE), and coefficient of variation (%) for 8 morphometric characters for *T. alpestris* females. P-paedomorphic individuals, M-metamorphic individuals, N-sample size.

| | | | L | L _{sv} | D | P _a | P _p | L _{cd} | L _{tc} | L _c |
|-----------------------------|-----------|-------|-------|-----------------|-------|----------------|----------------|-----------------|-----------------|----------------|
| Žegar (M)(N = 34) | \bar{X} | 82.68 | 47.03 | 24.63 | 15.62 | 15.65 | 39.60 | 8.20 | 5.94 | |
| | \pm SE | 0.88 | 0.49 | 0.35 | 0.15 | 0.19 | 0.50 | 0.09 | 0.06 | |
| | CV | 6.22 | 6.04 | 8.23 | 5.94 | 7.17 | 7.30 | 6.72 | 6.30 | |
| Grulovići (P)(N = 36) | \bar{X} | 82.89 | 43.09 | 24.88 | 15.59 | 15.41 | 40.98 | 9.44 | 5.34 | |
| | \pm SE | 0.74 | 0.58 | 0.26 | 0.13 | 0.12 | 0.48 | 0.08 | 0.06 | |
| | CV | 5.34 | 8.02 | 6.32 | 5.14 | 4.81 | 7.03 | 5.25 | 7.14 | |
| Pajića lokva (P)(N = 50) | \bar{X} | 78.51 | 43.19 | 24.32 | 14.37 | 14.67 | 38.98 | 7.70 | 4.74 | |
| | \pm SE | 0.44 | 0.24 | 0.19 | 0.12 | 0.11 | 0.29 | 0.05 | 0.04 | |
| | CV | 3.92 | 3.96 | 5.63 | 5.92 | 5.14 | 5.17 | 5.04 | 6.04 | |

Table 4. Collection localities, means (\bar{X}), standard errors (\pm SE), and coefficient of variation (%) for 8 morphometric characters for *T. alpestris* males. P-paedomorphic individuals, M-metamorphic individuals, N-sample size.

| | | L | L _{sv} | D | P _a | P _p | L _{cd} | L _{tc} | L _c |
|------------------------------|-----------|-------|-----------------|-------|----------------|----------------|-----------------|-----------------|----------------|
| Žegar (M) (N = 29) | \bar{X} | 74.90 | 43.18 | 21.45 | 15.61 | 15.86 | 36.34 | 7.88 | 5.72 |
| | \pm SE | 0.67 | 0.34 | 0.20 | 0.15 | 0.14 | 0.44 | 0.09 | 0.06 |
| | CV | 4.83 | 4.25 | 5.07 | 5.02 | 4.87 | 6.53 | 5.96 | 5.64 |
| Pajića lokva (P) (N = 26) | \bar{X} | 72.73 | 40.55 | 21.34 | 13.96 | 14.65 | 36.40 | 7.11 | 4.75 |
| | \pm SE | 0.65 | 0.33 | 0.29 | 0.15 | 0.18 | 0.41 | 0.07 | 0.05 |
| | CV | 4.54 | 4.17 | 6.99 | 5.51 | 6.34 | 5.05 | 4.88 | 5.87 |

means of CV values of all characters were compared.) The same trend was observed for some other smooth newt population (Tucić and Kalezić 1984).

Establishing a new smooth newt subspecies, *T. v. schreiberi*, Wolterstorff (1914) claimed that among other features individuals of this subspecies were characterized by small size. Though separate taxonomic position of the smooth newt populations from Ravni Kotari is now seriously in question, this Wolterstorff's statement seems to be still valid. Of analysed 5 population samples of *T. v. meridionalis*, 2 of *T. v. graecus* and 3 of *T. v. dalmaticus* (author's data unpubl.), and 11 population samples of nominotypical subspecies (Tucić and Kalezić 1984), only individuals of one population of *T. v. vulgaris* (From Obedska bara, near Beograd) were smaller in size than newts from Smilčić population sample.

Average values of eight size parameters of the analysed alpine newt population samples from Bukovica region, including the extent of variability of the analysed characters, are shown separately for females (Table 3) and males (Table 4). Only comparisons of paedomorphic individuals from Pajića Lokva and Grulovići to metamorphic individuals from Žegar were possible because of the complete absence or insufficient number of metamorphic or paedomorphic companions of the same population respectively.

Table 5. ANOVA F-ratio values for 8 morphometric characters obtained in comparisons of paedomorphic newts from Pajića lokva and Grulovići to metamorphic newts from Žegar locality.

^xP<0.05, ^{xx}P<0.01, ^{xxx}P<0.001

| Character | Pajića lokva × Žegar | | Grulovići × Žegar |
|-----------------|----------------------|--------|-------------------|
| | ♀♀ | ♂♂ | ♀♀ |
| L | 0.17 | 5.33 | 0.03 |
| L _{sv} | 76.37 | 30.22 | 6.87 |
| D | 0.73 | 0.01 | 0.24 |
| P _a | 38.79 | 61.71 | 0.01 |
| P _p | 22.98 | 28.04 | 1.12 |
| L _{cd} | 1.32 | 0.01 | 3.99 |
| L _{tc} | 23.52 | 46.68 | 90.06 |
| L _c | 276.72 | 140.85 | 43.21 |
| df | 83 | 54 | 69 |

Paedomorphic females from Grulovići were somewhat larger in size for most characters than metamorphic females from Žegar (Table 3). Statistically significant differences in this comparison appeared in head dimensions (Table 5); paedomorphic females had much wider and shorter head than metamorphic females. In comparison of paedomorphic females and males from Pajića Lokva to metamorphic females and males from Žegar, besides pronounced differences in characters connected with feeding (L_{tc} , L_c), statistically significant differences appeared for some overall size character (L_{sv}) and for limb lengths (Tables 3, 4 and 5). In respect to sex, the F-ratio values in comparison of paedomorphic individuals from Pajića Lokva to metamorphic newts from Žegar failed to repeat the pattern observed in Smilčić population sample of the smooth newt and in some other alpine newt populations with facultative paedomorphosis that differences in size are more pronounced in females than in males (Table 5). This may be the consequence of interpopulation instead of intrapopulation comparisons.

Differences in the level of variability of studied morphometric characters in the alpine newt population samples were not so drastic as in the smooth newt sample. Fore and hind limbs distance of females from Žegar was the most variable character ($CV = 8.2\%$), while total length of females from Pajića Lokva sample was the least variable character ($CV = 3.9\%$). In Žegar population sample females were more variable than the males of the same population taking into consideration all characters; difference was statistically significant, $t = 3.85$, $df = 14$, $P < 0.01$. This was not the case in Pajića Lokva population sample where males appeared to be somewhat (not statistically) more variable than females ($t = 0.73$, $df = 14$).

Discussion

The alpine newt (*Triturus alpestris*) is often considered as a highland and more continental species especially in southern parts of its range (e. g. Steward 1969; Arnold and Burton 1978). That it can be found in Submediterranean areas of Yugoslavia in unusual habitats and at relatively low altitudes is a fact acquired quite recently (Džukić and Kalezić 1984; Schmidtler 1988). The lowermost pond where the alpine newt occurred in Bukovica region is situated at the altitude of 80 m (Žegar). The ponds with the alpine newts in this region are on the substrate of exposed karst with scanty stands of crack plant dwellers. The populations in question have a distinctly peripheral distribution relative to more continental alpine newt populations and occur in extremely arid environment supposedly unoccupied by this species elsewhere. Undoubtedly, the presence of *Triturus alpestris* in Bukovica region is owe to the vicinity of mountain Velebit where colonies of the alpine newt are common.

Schmidtler (1988) stated that the presence of the alpine newt in Adriatic Mediterranean climate zone might be facilitated by the absence of its important competitor – smooth newt. This might be true for the whole Bukovica region where none of the smooth newt individuals were found. On the contrary, in Ravni Kotari region only smooth newt populations occur. What makes this allotopic pattern of newts distribution in Bukovica and Ravni Kotari? Why this is not so in a nearby Lika region where a number of syntopic populations of *T. alpestris* and *T. vulgaris*, together with *T. cristatus*, can be found? Why the smooth newt does not occur in Bukovica region while in Montenegro Submediterranean areas populations of this species are quite numerous in the aquatic habitats similar to those in Bukovica? We do not have straightforward answers for these questions but some relevant, more or less theoretical, considerations may shed light upon biological process(es) which lead to allotopic or syntopic distribution patterns.

In the theory of the competition between related species, two principles can be evoked: (1) the competitive exclusion principle (Gause 1934), and (2) the principle of coexistence (Den Boer 1980). According to competitive exclusion principle when two species that have similar requirements for resources cooccur, one species eventually outcompetes and causes the extinction of the other. The fact of occupation of separate habitats of two newt species does not ultimately prove the existence of their competi-

tion. In fact, within the genus *Triturus* there is little evidence for interspecific competition during the aquatic phase of adult lifetime (Szymura 1974; Griffiths 1987). Resource partitioning with respect to some of niche dimensions can occur as was found for *Triturus cristatus* and *Triturus marmoratus* (Schoorl and Zuiderwijk 1981; Zuiderwijk and Bouton 1987).

There are numerous autecological studies relating to habitat selection, diet and timing of seasonal and diel activities of the smooth newt (e.g. Griffiths 1987; Verrell and Halliday 1985). The relatively wide ecological amplitude of *T. vulgaris* is well known (c.f. Dolmen 1981 for references). Such data for the alpine newt are much less numerous but it seems that it can breed in a variety of habitats as well. These newts frequently coexist in various continental habitats situated at different altitudes (in Yugoslavia from 250 m to 1800 m above sea level; author's data, unpubl.). This undoubtedly indicates that some degree of niche overlap between smooth and alpine newts exists. However, no quantitative attempts have yet been made to compare the niches of these newts. The coexistence of two species with niche overlap may depend upon limited supply of resources of any kind. We do not know whether the levels of carrying capacity of ponds in Bukovica and Ravni Kotari differ from those in more continental areas. So far, we cannot prove that primarily ecological factors shaped the observed countercurrent vertical distribution pattern of the smooth newt and the alpine newt, or that such distribution is simply a remnant of some historical events (Pleistocene glaciations, for example).

According to Hadži (1926, 1931, 1935), Bukovica and Ravni Kotari belong to the Adriatic zoogeographic subprovince (*Adriatica*). (Zoogeographical zones of Yugoslavia were established on the basis of terrestrial animal distribution.) A narrow zone along the coast is a part of this subprovince (*pars litoralis*) which extends all along the coast. The other part of this subprovince is *pars carsica*. Bukovica and the most of Ravni Kotari appertain to the Velebit's part of *pars carsica* — *pars velebitana* which southeastern boundary mainly follows the river Krka (Fig. 1). Adjacent part of *pars carsica* to *pars velebitana* is *pars zagoriensis*. That such biogeographical boundary is valid confirms Fukarek's (1977) phytogeographical analysis, as well as distribution patterns of some members of herpetofauna (e.g. Szyndelar 1984). Also, the southeastern edge of the range of *Lacerta horvathi* coincidence to the above mentioned boundary; the same is with the northwestern border of the areals of *Lacerta oxycephala* and *Lacerta mosorensis* (Džukić unpubl.). Discontinuity of fauna of these two regions is also proved by the distribution of the smooth newt taxa in areas in question. In Ravni Kotari isolated populations of nominotypical subspecies occur. This part of the smooth newt range appears to be separated from the core of *T. v. vulgaris* distribution, which covers the most part of Yugoslavia, by the zone of alpine newt in Bukovica. In *pars zagoriensis* another smooth newt taxa occur; according to Kolombatović (1907), Mertens and Wermoth (1960) and Diesner (1966) it is *T. v. dalmaticus*, while Schmidtler and Schmidtler (1983) claimed that this was a zone of hybridization of *T. v. vulgaris* and *T. v. graecus*. As far as we know, this is the first evidence that some newt taxa proved (or disproved) discontinuity in fauna elements.

The first discovery of the alpine newt paedomorphosis in Submediterranean area of Yugoslavia (Nevesinjsko Polje, Džukić and Kalezić 1984), and four additional findings of *T. alpestris* with facultative paedomorphosis in Bukovica proved that the Submediterranean area is an important centre of such heterochronic phenomenon. The same is with the smooth newt species. Paedomorphosis in *T. vulgaris* in the Submediterranean area of Yugoslavia is known from southwestern part of Montenegro (Džukić 1981, Kalezić and Džukić 1985, 1986), from southeastern part of Montenegro (near Ucinj) and from Sinjsko Polje (author's data, unpubl.), from Zagora (Kolombatović 1907, 1908), and from Ravni Kotari (this paper). Paedomorphosis appearance in Submediterranean was considered in the light of fragmented population structure and flush-crash population cycles presumably characterizing the population dynamics of the newt populations in this area. The maintenance of paedomorphosis was attributed to hostile terrestrial newt habitats in Submediterranean and/or some mechanism(s) which minimize intraspecific competition through an increase in phenotypic variability (see Kalezić and Džukić 1985 and references therein). We believe that our analysis of morphometric varia-

bility of paedomorphic and metamorphic newts from Bukovica and Ravni Kotari, together with the same analyses on other paedomorphic newt populations (Tucic et al. 1985; Kalezić et al. 1989), proved the last statement. Differences in morphometric characters between paedomorphic and metamorphic individuals appeared to be considerable for characters connected with feeding abilities. This might indicate some degree of food selection by prey size in aquatic assemblages of transforming and nontransforming newt individuals of the same population. However, the above supposition remains to be tested. If it is so, facultative paedomorphosis would appear as an evolutionary device for minimizing intraspecific competition as has been earlier suggested by Wilbur and Collins (1973).

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